Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha

Leach, K., Montgomery, W. I., & Reid, N. (2015). Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha. *Mammal Review*, *45*(2), 88-102. https://doi.org/10.1111/mam.12035

Published in:
Mammal Review

Document Version:
Peer reviewed version

REVIEW

Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha

Katie LEACH* *Quercus, School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, Northern Ireland. E-mail: kleach01@qub.ac.uk*

W. Ian MONTGOMERY *School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, Northern Ireland. E-mail: i.montgomery@qub.ac.uk*

Neil REID *School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, Northern Ireland and Institute for Global Food Security (IGFS), Queen's University Belfast, Belfast, BT9 5BN, Northern Ireland. E-mail: neil.reid@qub.ac.uk*

* Correspondence author

ABSTRACT

1. In addition to abiotic determinants, biotic factors, including competitive, interspecific interactions, limit species' distributions. Environmental changes in human disturbance, land use and climate are predicted to have widespread impacts on interactions between species, especially in the order Lagomorpha due to the higher latitudes and more extreme environmental conditions they occupy.
2. We reviewed the published literature on interspecific interactions in the order Lagomorpha, and compared the biogeography, macroecology, phylogeny and traits of species known to interact with those of species with no reported interactions, to investigate how projected future environmental change may affect interactions and potentially alter species' distributions.
3. Thirty-three lagomorph species have competitive interactions reported in the literature; the majority involve hares (*Lepus* sp.) or the eastern cottontail rabbit (*Sylvilagus floridanus*).

Key regions for interactions are located between 30-50°N of the Equator, and include eastern Asia (southern Russia on the border of Mongolia) and North America (north western USA).

4. Closely related, large-bodied, similarly sized species occurring in regions of human-modified, typically agricultural landscapes, or at high elevations are significantly more likely to have reported competitive interactions than other lagomorph species.

5. We identify species' traits associated with competitive interactions, and highlight some potential impacts that future environmental change may have on interspecific interactions. Our approach using bibliometric and biological data is widely applicable, and with relatively straightforward methodologies, can provide insights into interactions between species.

6. Our results have implications for predicting species' responses to global change, and we advise that capturing, parameterizing and incorporating interspecific interactions into analyses (for example, species distribution modelling) may be more important than suggested by the literature.

Submitted: 8 September 2014

Returned for revision: 21 October 2014

Revision accepted: 12 January 2015

Editor: KH

Key words: Biotic interactions, climate change, competition, leporids, pikas.

Running head: Competitive interactions in the order Lagomorpha

INTRODUCTION

Biotic interactions underpin a wide range of ecosystem processes and can occur between individuals of the same species (intraspecific interactions), or among individuals belonging to different species (interspecific interactions; Connell 1983, Chase et al. 2002). Interactions can take place at the local scale, for example, predation, parasitism, competition, and disturbance, or at the regional scale, for example, dispersal, speciation, extinction, and expansions or contractions of species' ranges (Cornell & Lawton 1992, Amarasekare 2003). Competitive interactions are variously defined, but most definitions incorporate limited resources, for example: "the negative effects that one organism has upon another by consuming or controlling access to a resource that is limited in availability" (Keddy 2001). Strong competitive interspecific interactions at the same trophic level are likely to be due to occupied or partially occupied niche space which influences species' coexistence (Cornell & Lawton 1992). Competition can be symmetrical, whereby there are equivalent negative effects, or asymmetrical, whereby there is a clear winner or loser (Connell 1983, Schoener 1983). Three mechanisms are known: (i) interference competition is when an individual directly affects another, for example, by using aggression (Birch 1957); (ii) exploitation competition is when individuals interact indirectly, usually competing for a common, limited resource (Keddy 2001); and (iii) apparent competition is when two individuals that do not compete directly for resources affect each other indirectly, by being prey for the same predator (Chaneton & Bonsall 2000, Hatcher et al. 2006, DeCesare et al. 2010).

Competitive interactions tend to produce biogeographical patterns in species' distributions. Competing species may meet at a sharp boundary with little or no overlap, whereas non-competing species' ranges may show complete overlap (Flux 2008). Parapatry is when two species have separate but contiguous ranges, with no physical barrier between them, and only co-occur, if at all, in a narrow contact zone (Bull 1991, Gutiérrez et al. 2014). Ranges of

allopatric species are separated by a geographic barrier and, therefore, there can be no interspecific interaction. Sympatric species share the same geographical space, but may compete for access to similar habitats or resources. Alternatively, species occupying overlapping niches may not compete, so that their coexistence is possible due to the partitioning of resources. Exploitation competition may be evident if, for example, habitat use between species is comparable; abrupt habitat shifts at their point of contact in sympatry are likely to mirror the response to competition (Vidus-Rosin et al. 2011).

Traits of competitively interacting species have been studied in great detail (e.g. Schoener 1982, Luiselli 2006). Phylogenetic relatedness and its association with competition are often studied. Darwin (1859) suggested that closely related species are more likely to exhibit competition because they occupy similar ecological niches. Close relatedness of interacting species has since been shown experimentally (Violle et al. 2011), but does not hold for some taxa, for example, green algae (Venail et al. 2014). Species with larger body masses are more competitive because they are able to utilise a larger share of resources (Brown & Maurer 1986) and similarly sized species are typically more likely to interact (Leyequien et al. 2007). Environmental traits can also influence competitive interactions, for example, competition is more likely in urban environments with higher human population densities (Shochat et al. 2006), and past climatic changes have probably caused large impacts on species' distributions and, therefore, on interspecific interactions (Koblmüller et al. 2012). Interactions between species are more common at high elevations (Jankowski et al. 2010), perhaps due to limited resources there, and are more vulnerable to change due to the predicted effects of climate change at such elevations (Chen et al. 2011), potentially changing species' ranges both directly and indirectly. Thus, environmental change, caused by human disturbance, changes in climate, or changes in land use, may have direct or indirect effects on the strength of biotic interactions, thus informing our interpretation of their likely influence on species' distributions.

97 Interactions between species are extremely difficult to identify and quantify in the wild.
98 Consequently, the impacts of global change on biotic interactions have rarely been studied
99 (McCann 2007), but they are likely to be significant, due to related changes in phenology,
100 behaviour, physiology, abundance and the co-occurrence of multiple species throughout biomes
101 (e.g. Tylianakis et al. 2008). In the majority of cases, interactions are inferred from parapatry or
102 species replacement, but this inference is not conclusive, and interactions could be a result of
103 hybridization or adaptation to different habitats with no geographic overlap (Huey 1979).
104 Competitive interspecific interactions may be altered by changes in dominant plants or animals
105 under future environmental change; for example, increases in mean global temperatures could
106 affect seed dehiscence times and change competition between mammalian seed predators and
107 invertebrate seed dispersers (Ness & Bressmer 2005). In a hypothetical situation in which
108 species A, B and C are positioned along a resource gradient, with species A occupying the upper
109 end (a region of high resource availability), species C occupying the lower end (a region of low
110 resource availability), and species B occupying a niche between the two, any response to future
111 environmental change involving an increase in the availability of resources may lead to selection
112 favouring the more extreme species (A and C) and, hence, may lead to the expansion of their
113 distributions (impacting species B). For example, species B could broaden its niche space, or
114 new species could invade and occupy niche vacancies left by shifts in species A and/or C.
115 However, if environmental change were to reduce the availability of resource types, the ranges
116 of all three species may contract, which could increase the intensity of competition, and possibly
117 lead to local extirpations at their contact zones, or total extinction(s) (Post 2013).

118 Lagomorphs are an important group of mammals economically and scientifically, as they are
119 a major human food resource, model laboratory animals, valued game, significant agricultural
120 pests, and key elements in food chains that provide scientific insights into entire trophic systems
121 (Chapman & Flux 2008). Competition among species in the order Lagomorpha can involve

122 interference or exploitation for food or shelter (Vidus-Rosin et al. 2008). Interspecific
123 competition is common between lagomorph species and is often precipitated by the introduction
124 of non-native species (e.g. the European rabbit *Oryctolagus cuniculus*, the European hare *Lepus*
125 *europaeus*, and the eastern cottontail *Sylvilagus floridanus*), leading to suppression or expulsion
126 of native lagomorphs from certain habitats due to dominant behaviour and adaptive capabilities
127 of the antagonist (Hackländer et al. 2008). Intraspecific competition in lagomorphs (Somers et
128 al. 2012) and competition with other herbivores (Hulbert & Andersen 2001, Bakker et al. 2009),
129 on the other hand, has been rarely reported in the literature.

130 Lagomorphs are likely to be affected by environmental change because they occupy a wide
131 range of environmental conditions in all continents except Antarctica, and because they are
132 found at extreme elevations, from sea level to >5,000 m, and at very high latitudes, from the
133 Equator to 80°N (Chapman & Flux, 2008). A quarter of lagomorph species are listed in the
134 International Union for Conservation of Nature's (IUCN) Red List of Threatened Species
135 (www.iucnredlist.org); a notable number of species have highly restricted ranges, including 14
136 listed under the IUCN's Criterion B, with an extent of occurrence estimated to be less than
137 20,000 km^2. Environmental change is predicted to have significant effects on lagomorphs,
138 especially changes in climatic conditions (Ge et al. 2013, Mills et al. 2013), land use (Fa & Bell
139 1990) and human disturbance (Schmidt et al. 2012), and is likely to have significant effects on
140 lagomorph-lagomorph interactions. Research on parapatric hare species in Europe (Acevedo et
141 al. 2012) showed that, under future climate scenarios, the Iberian hare *Lepus granatensis* is
142 likely to be the beneficiary in competition with the European hare in their zone of contact in
143 Northern Iberia, and interactions between the mountain hare *Lepus timidus* and the European
144 hare are expected to contribute to the decline of the former in areas of co-occurrence in Northern
145 Europe (Acevedo et al. 2012), for example, in Sweden (Thulin 2003) and Ireland (Reid 2011).

We collate, review and assess all published data on lagomorph-lagomorph interactions, from both experimental evidence and inference from parapatry or species replacement, and examine the potential relationships between the environment and species' traits within different types of interaction. We aim to investigate how future environmental change may affect such interactions and potentially alter species' distributions. We predict greater competition between lagomorph species at higher elevations, due to restrictions in suitable habitat and in the range of potentially interacting species found in mountainous terrain, and in human-converted habitats, which are frequently inhabited by lagomorphs due to the availability of food (e.g. grasses or crops) and shelter (e.g. field margins and hedgerows providing cover) there. We expect the restricted range of food available in and the uniformity of anthropogenic landscapes to intensify competitive interactions. We also hypothesize that competitive interactions are more likely to occur between closely related species (i.e. those with shorter-than-average pairwise phylogenetic distances) with a small difference in body mass (i.e. those relatively similar in size). We use a combination of bibliometric analyses and biological data to assess traits associated with competitive interactions in an entire mammalian order, the Lagomorpha.

METHODS

Capturing competitive interactions

In the taxonomy we adopt, the Lagomorpha comprises 87 species in two families: the Ochotonidae consists of one monotypic group in the genus *Ochotona* containing 25 species of small, social pikas found at high latitudes, and usually high elevations; the Leporidae has 32 species of large, solitary, cursorial hares and jackrabbits in the genus *Lepus* and 30 species of medium-sized, semi-social, fossorial rabbits in 10 genera (Chapman & Flux 2008; *Ochotona nigritia* and *Ochotona gaoligongensis* were classed as morphs of *Ochotona forresti*, *Ochotona muliensis* as a morph of *Ochotona gloveri*, *Ochotona himalayana* as a morph of *Ochotona*

roylei and *Ochotona huangensis* as a morph of *Ochotona thibetana* following the taxonomic expertise of Dr Andrey Lissovsky, Zoological Museum of Moscow State University).

Data on interspecific interactions involving only lagomorphs were captured using the Web of Knowledge, searched using the terms "lagomorph AND interaction" or "lagomorph AND competition". Additional search terms included pairwise combinations of all species whose IUCN range polygons overlapped (using both scientific and common names) to identify the possibility of interactions not returned in the initial search. All 3,741 possible pairs of the 87 species in our taxonomy were classified as: (i) allopatric, i.e. exhibiting no range overlap, and lacking any published evidence of interspecific interactions; (ii) sympatric (i.e. with partially coincident geographical ranges, defined as overlap in their IUCN range polygons), but with no known interaction; or (iii) sympatric with interaction reported in the literature. Competitive interactions were classed as either exploitation or interference.

Information on interactions may be biased by body size or taxonomic group due to variable research effort (Brooke et al. 2014), and some pairwise interactions are likely to be undocumented in the literature to date; thus, the current study may have been vulnerable to type II errors or false negatives in identifying species' interactions. Moreover, there may have been a bias towards species showing interactions, due to researchers' preference for reporting significant effects: so-called 'publication bias' (Connell 1983). To take this potential bias into consideration, instead of assuming no competition between species for which there was no evidence of interaction, we defined category ii) as 'sympatric with no known interaction'.

Spatial analysis

The geographical range (based on the IUCN polygon) for each of the 33 species that had at least one documented interaction with another species was rasterised in ArcGIS 10.2 (ESRI, California, USA) at 30 arc-second resolution (~1km^2 grid cells), with a value of 1 for presence

194 and 0 for absence. The invasive range of the eastern cottontail in Italy was not included because
195 IUCN polygons were only available for its native distribution. Rasterised data were summed to
196 show the global distribution of possible interactions between species known to interact with at
197 least one other species. Mean elevation (m) and latitude (°) occupied by each pair of species
198 known to interact were calculated at 30 arc-second resolution (~1km^2 grid cells).

199 **Species' traits and environmental data**

200 Phylogenetic distance, the amount of time since the most recent common ancestor of both
201 species existed (Vellend et al. 2011), as a proxy for phenotypic differences between two species
202 (Cavender-Bares et al. 2009), was quantified for each pair (including allopatric, sympatric with
203 no known interaction and sympatric with interaction), to investigate whether closely related
204 species were more likely to interact competitively. A lagomorph phylogeny was extracted from
205 the mammalian supertree provided by Fritz et al. (2009). Likely clade membership for five
206 species not included in this phylogeny was determined from Ge et al. (2013), and missing tips
207 were grafted on using an expanded tree approach (Day et al. 2008). Pairwise phylogenetic
208 distances were calculated using the 'ape' package (Paradis et al. 2014) for R version 3.1.1.

209 Species' traits, including body mass (grams) and human population density (people/km^2)
210 within each species' range, were taken from the PanTHERIA database (Jones et al. 2009).
211 Ecoregional climatic stability data was provided by Takuya Iwamura (Iwamura et al. 2013), and
212 was defined as "the proportion of an ecoregion which is predicted to be climatically stable under
213 [future] climate change." The climatic stability index is calculated by estimating the overlap
214 between present and future climatic envelopes for each ecoregion, using results from seven
215 global circulation models. It ranges from 0 (no overlap between current and future climates) to 1
216 (complete overlap and high robustness to climate change; Watson et al. 2013).

For each species, the percentage of occurrence records in human-converted habitats was included as a coarse measure of the threat to each species from human activities, following Hoekstra et al. (2005). Converted habitats included cultivated or managed land and artificial surfaces; areas were derived from a modified version of the Global Land Cover 2000 dataset (Anonymous, 2003). The occurrence data used in this calculation comprised 41,874 records that were either downloaded from the Global Biodiversity Information Facility data portal (data.gbif.org), collated from experts or members of the IUCN Species Survival Commission Lagomorph Specialist Group, and/or extracted from the literature for data-deficient species. Taxonomic accuracy was ensured by checking all records against the latest IUCN taxonomy; if names did not match after cross-referencing with taxonomic synonyms and previous names, records were rejected. Spatial data accuracy was ensured by removing any records that were obviously erroneous because they fell outside the extent of the IUCN geographic range polygon. In addition, occurrences recorded with a spatial resolution of >2km were removed, and duplicate records were eliminated. Species' traits considered (examined) but not included in the analysis are listed in Appendix S1.

Statistical analyses

A linear regression was performed in R version 3.1.1 to test the relationship between the dependent variable, elevation (m), and the number of possible pairwise interactions (rasterised data from the *Spatial analysis* section). A Generalized Linear Model was used to evaluate differences between pairs of species allocated to the three interaction types: (i) allopatric, (ii) sympatric with no known interaction and (iii) sympatric with interaction, using a number of species' traits as explanatory variables (phylogenetic distance, mean body mass, similarity in body mass, mean ecoregional climatic stability, mean human population density and mean percentage of occurrence records in human-converted habitats).

241 **RESULTS**

242 **Spatial patterns of interspecific interactions**

243 Of the 3,741 possible pairs between the 87 species of lagomorph, 3,489 were classed as
244 allopatric, 219 were classed as sympatric with no known interaction, and 33 were classed as
245 sympatric with documented interaction; of the 33 species involved in the 33 documented
246 interactions, nine were pikas, eight were rabbits and 16 were hares (Table 1). The distribution of
247 documented interspecific interactions was not uniform but clustered in eastern Asia (exclusively
248 pikas) and North America (rabbits, hares and jackrabbits; Fig. 1a). Six of the interactions
249 involved interference competition, and five of these (83%) involved the eastern cottontail. The
250 global distribution of possible pairwise interactions between lagomorph species (Fig. 1b) showed
251 that in large areas (~69% of the total global range of the order Lagomorpha), no documented
252 pairwise interactions exist (Fig. 1c); lagomorph species were 2.2 times more likely to occur in
253 allopatry than in sympatry, and 3.1 times more likely to be involved in just one pairwise
254 interaction than in multiple interactions. The mean number of potential pairwise interactions
255 globally was 1.51 ± 0.78 (SD). Only small areas of the globe contained the highest
256 concentrations of possible interactions; for example, there were six possible pairwise species
257 interactions in a 6,000 km^2 area in southern Russia on the border of Mongolia (Fig. 1c), with
258 interactions clustered around 30-50°N of the Equator (Fig. 1d). There was a significant positive
259 association between the number of possible pairwise interactions and elevation ($F_{3, 49917}$= 731.8,
260 p<0.001; Fig. 2).

261 **Linking interactions to species' traits and environmental change**

262 Sympatric pairs of species with documented pairwise interactions had significantly shorter
263 phylogenetic distances between them than pairs of species that occurred in sympatry but had no
264 known interaction ($F_{2, 3738}$ = 19.8, p<0.001; Fig. 3a, see Appendix S2). Thus, within the order

Lagomorpha, sympatric species with documented competitive interactions were 2.3 times more closely related than sympatric species with no known interaction.

The mean body mass of pairs of interacting sympatric species was significantly greater ($F_{2, 3738} = 22.3$, $p<0.001$) than that of pairs of sympatric species that had no known interaction (Fig. 3b, Appendix S2). The mean body mass of pairs of allopatric species was lower than both. However, whilst interacting species tended to be heaviest, analysis of the difference in body mass between species in each pair showed that pairs of interacting species were significantly closer in mass than pairs of allopatric species and sympatric species with no known interaction (Fig.3c, Appendix S2).

There was no difference in mean ecoregional climatic stability between the pairwise interaction types ($F_{2, 3738} = 0.03$, $p=0.969$; Fig. 3d, Appendix S2). The mean ecoregional climatic stability index value for the order Lagomorpha was 0.46 ± 0.14, which is similar to, but slightly higher than, the global average of 0.42 ± 0.03.

Pairs of sympatric species were more likely to occur in regions of high human population density, but due to the variability in human population density in regions supporting lagomorphs, the difference between sympatric groups was not significant (Fig. 3e, Appendix S2). However, there was a significant difference in mean human population density between the ranges of pairs of allopatric species and those of sympatric species with a known interaction ($F_{2, 3738} = 5.02$, $p<0.001$; Fig. 3e). Interacting pairs of sympatric species occurred significantly more frequently in human-converted habitats than pairs of sympatric species with no known interaction ($F_{2, 3738} = 6.3$, $p=0.002$), and pairs of sympatric species with no known interaction were significantly more frequently found in human-converted habitats than pairs of allopatric species ($F_{2, 3738}=6.3$, $p=0.002$; Fig. 3f, Appendix S2).

REVIEW AND DISCUSSION

Closely related, large-bodied, similarly-sized species occurring in regions of human-modified, typically agricultural landscapes, or at high elevations, were significantly more likely to exhibit competitive interactions than other species within the order Lagomorpha. The greatest changes in species' ranges are likely to occur either at high elevation, where the effects of climate warming are pronounced (Chen et al. 2011), or in human-modified habitats, which are already subject to significant threats and pressures (McCarthy et al. 2010). This suggests that interacting species, which are found more commonly in human-modified habitats and at high elevation, are likely to be highly susceptible to future environmental changes. Moreover, the average ecoregional climatic stability index for regions inhabited by lagomorphs, although slightly higher than the global average, indicates only medium robustness of those regions to future changes in climatic conditions. Larger mammalian species are predicted to be especially vulnerable to future climatic changes (McCain & King 2014). Many of the responses to climate change in large mammals, e.g. the Eurasian elk *Alces alces*, are in fact positive, but large species are nevertheless vulnerable to change. In addition, we expect closely related species to show similar responses to environmental change, although idiosyncratic responses are predicted to be more likely (Tafani et al. 2013).

Experimental evidence of competition

Thirty-three pairwise interspecific interactions were identified within the order Lagomorpha, but the evidence for the majority of these competitive interactions was from opportunistic, isolated field observations inferred from parapatry or species replacement. Only one study to date (Probert & Litvaitis 1996), provides experimental evidence of competition in lagomorphs: interference competition between the eastern cottontail and the New England cottontail *Sylvilagus transitionalis*, due to their utilisation of the same habitat and food resources (e.g.

313 Johnston 1972), has led to the expansion of the former and a decline in abundance of the latter. It
314 is possible that the eastern cottontail is a better competitor than the New England cottontail due
315 to inbreeding in transplanted locations which, by increasing the genetic variability of offspring,
316 has functionally enabled occupation of a broad range of habitats (Litvaitis et al. 2008) and also
317 because it is approximately 20% larger. The experimental trial by Probert and Litvaitis (1996),
318 however, showed that eastern cottontails were dominant in only 42% of trials, suggesting that
319 factors other than physical dominance may explain their colonisation of habitats. Eastern
320 cottontails are likely to be dominant because they use open habitats (Smith & Litvaitis 2000),
321 can detect predators at greater distances (Smith & Litvaitis 1999), and have better dispersal
322 capabilities (Probert & Litvaitis 1996) than New England cottontails.

323 Interference competition, as recorded by Probert and Litvaitis (1996), is attributable only to a
324 very small proportion of reported pairwise interactions between lagomorph species. This
325 suggests that most species lack aggressive antagonistic behaviour towards other lagomorphs.
326 Most notably, the eastern cottontail exhibits strong evidence for interference competition by
327 commonly displacing other species from shared habitats (Litvaitis et al. 2008). Our results
328 suggest that the eastern cottontail occupies a region of average climate stability (~0.36), with
329 higher than average mean human population density (267 individuals/km^2) and higher than
330 average occurrence within human-converted habitats (44%). Occupation of areas vulnerable to
331 anthropogenic change may lead to heightened aggression in competitive interactions between the
332 eastern cottontail and other lagomorphs, e.g. pygmy rabbits *Brachylagus idahoensis*, brush
333 rabbits *Sylvilagus bachmani,* forest rabbits *Sylvilagus brasiliensis*, mountain cottontails
334 *Sylvilagus nuttallii* and New England cottontails, but further comparative analysis of species'
335 traits may be required to identify the mechanisms behind its uniquely aggressive, competitive
336 interactions.

337

338 **Inferred competition based on parapatry or species replacement**

339 Competitive interactions are not easily identified in the wild, and even when they are, most
340 competition is inferred from parapatry or species replacement. Due to limited data, we
341 considered two species to be competitively interacting even if there was only one record
342 providing supporting evidence, i.e. either an experimental study or inference from parapatry or
343 species replacement. However, the weaknesses of inferring competition should be noted.
344 Parapatric distributions and species replacement are consistent with intraspecific competition,
345 but evidence is far from conclusive. Huey (1979) states that parapatry is often used as evidence
346 for competition, and parapatric distributions can in fact result from intense interspecific
347 competition, but they may also arise from hybridization or from adaptation of species to
348 different habitats that do not overlap geographically. Nevertheless, with scarcely any
349 experimental demonstration of competitive interactions in lagomorphs, information on parapatric
350 distributions and species replacement is all we have at present to review competition within the
351 order.

352 Hares of the genus *Lepus* are typically allopatric, but in a few notable cases they exhibit
353 parapatry. For example, in Europe there are five *Lepus* species: the Apennine hare *Lepus*
354 *corsicanus* and broom hare *Lepus castroviejoi* have restricted allopatric ranges, whereas the
355 European hare, mountain hare and Iberian hare have much wider ranges. Competition between
356 the latter three species is asymmetrical and in most cases the ranges are parapatric (Acevedo et
357 al. 2012). In the contact zone between Iberian and European hares, there is a decrease in
358 abundance of the latter (Gortázar et al. 2007), the European hare competes with the Apennine
359 hare (Angelici et al. 2008) and there tends to be contraction of mountain hare ranges, in extent
360 and elevation, in contact zones with the European hare (Thulin 2003, Reid 2011). In most of the
361 European hare's native range, the mountain hare seems to be restricted to high elevations and
362 forests, as it is driven away from lowland grassland plains (Thulin 2003, Flux 2008), but in

363 Ireland, Finland, Russia and Sweden, the European hare, which was introduced in the late 19th
364 and early 20th centuries, is found in sympatry with the mountain hare (Flux 2008). In Ireland,
365 introduced European hares and endemic Irish hares *Lepus timidus hibernicus* occupy similar
366 habitats in sympatry (Reid & Montgomery 2007). They would probably show strong
367 interspecific competition if resources were limiting (Reid 2011), but this is highly unlikely as the
368 majority of available habitat is grassland and thus optimal for both species. Nevertheless, the
369 European hare has actively displaced the Irish hare within its core invasive range, creating a
370 zone of European hare allopatry (Caravaggi et al. 2014).

371 'Extinction by hybridization' was originally described by Rhymer and Simberloff (1996) as a
372 possible effect of hybridization between native and introduced species. If there were a large
373 number of hybrid events between female mountain hares and male European hares, then species-
374 specific litters would be lost in mountain hare populations, causing a loss of range and decline in
375 population density (Thulin 2003). In Sweden, where the two species hybridize in sympatry, the
376 mitochondrial DNA (mtDNA) from mountain hares is transferred to European hares, but this
377 pattern gradually disappears in areas of allopatry (Thulin & Tegelström 2002). Only one
378 researcher to date (Lind 1963) has examined competition between mountain hares and European
379 hares; competitive exclusion of mountain hares and significant differences in food preference
380 and habitat utilisation were found. However, European hares and mountain hares have often
381 been observed feeding side by side (Hewson 1990).

382 Species displacement through hybridization is not a new phenomenon restricted to secondary
383 contact after anthropogenic introductions of alien species into the ranges of old adversaries;
384 'ancient hybridisation' is prevalent within the order Lagomorpha such that many species actually
385 share mitochondrial or nuclear haplotypes revealing the 'ghosts of a hybrid past' (Paulo Célio
386 Alves, *pers. comms.* citing Wilson & Bernatchez 1998). Mountain hare mtDNA lineages are
387 found throughout Europe within European hares, Iberian hares and broom hares (Melo-Ferreira

et al. 2009). Such ancient hybridization is likely to have occurred during the last glacial maximum when the mountain hare's range would have extended further south than today. Moreover, European hares, Iberian hares and Apennine hares are also known to have hybridized in ancient times (Pietri et al. 2011). The phenomenon is pervasive, being present also in Asia (Liu et al. 2011) and North America. For example, snowshoe hare *Lepus americanus* mtDNA lineages in the Greater Pacific Northwest exhibit hybrid introgression from black-tailed jackrabbits *Lepus californicus*,, despite the minimal overlap of their current geographic ranges (Cheng et al. 2014, Melo-Ferreira et al. 2014). For the purposes of this study, ancient hybridization and introgression will not be considered any further as they do not represent on-going competitive behavioural interactions.

The majority of competitive interactions occurred between hares in the genus *Lepus* and involved a few key species, e.g. the European hare. Replacement of white-sided jackrabbits *Lepus callotis* by black-tailed jackrabbits and desert cottontails *Sylvilagus audubonii* has been observed (Best & Henry 1993); antelope jackrabbits *Lepus alleni* have been replaced by black-tailed jackrabbits in some habitats (Chapman & Flux 1990); snowshoe hares in Wisconsin, USA were replaced by white-tailed jackrabbits (Leopold 1947); and white-tailed jackrabbits were replaced by black-tailed jackrabbits (Flinders & Chapman 2003). The Abyssinian hare *Lepus habessinicus* and the European hare replace the cape hare *Lepus capensis* in some habitats (Chapman & Flux 1990; Flux 2008), but the Abyssinian hare has been replaced by the African savannah hare *Lepus microtis*, scrub hare *Lepus saxatilis*) and Ethiopian hare *Lepus fagani* in others (Chapman & Flux 1990). The African savannah hare is replaced by the scrub hare (Flux 2008), and the Manchurian hare *Lepus mandshuricus* and European hare are replaced by the Tolai hare *Lepus tolai* in Russian Asia (Fadeev 1966, Chapman & Flux 1990, Smith & Xie 2008, Sokolov et al. 2009). Competition amongst hares is inferred in many cases because a species is observed occupying the preferred habitat of another species in its absence, but it can also be

413 inferred due to the rare and transient nature of sympatric hare co-occurrence (Flux 1981). Hare
414 species often exhibit parapatric distributions and only tend to occur, if at all, temporarily in the
415 same habitat (Acevedo et al. 2012). Despite a lack of any experimental demonstration of
416 competitive exclusion in lagomorphs, this may nevertheless be a very powerful determinant of
417 geographical and local ranges (Flux 1981, Thulin 2003).

418 Large areas, globally, were occupied by lagomorphs for which there was no evidence of
419 interaction, suggesting that allopatry or parapatry is the usual situation, and that interspecific
420 contact is globally restricted and occurs only in relatively narrow contact zones. However, our
421 spatial analysis would not reveal that species could occupy the same range but be functionally
422 separated by habitat, e.g. mountain hares and European hares are separated by elevation within
423 parts of their contact zone (Thulin 2003). Thus, not all sympatric species will have the
424 opportunity to interact directly and, if they do, interactions may occur in a smaller range than
425 that suggested by our spatial analysis. In addition, population dynamics rather than competition
426 may cause a decline in the abundance of one species, leading to movement of the more abundant
427 species and hence replacement of one species by another in a particular habitat.

428 Hares and rabbits frequently co-occur, but rarely interact. The European hare and the
429 European rabbit form one of the most commonly studied and observed systems with respect to
430 competition. Before anthropogenic introductions, the European hare was restricted to central
431 Europe and the Asian steppes, and the European rabbit to the Iberian Peninsula (Flux 1994), but
432 overlap in the ranges of these two species is now widespread, and coexistence occurs in many
433 introduced populations (Flux 2008). Allopatry is seen at regional scales due to habitat
434 preferences (e.g. Petrovan 2011), and there is widespread belief that the species avoid each other
435 (e.g. Cox 1976). However, in most areas of their range they graze side by side, showing
436 significant dietary overlap (e.g. Katona et al. 2004). Various reports from the early 20th century

note physical attacks of rabbits on hares both in captivity and in the wild (Gayot 1868, Millais 1906), but more recent observations indicate that aggressive antagonism is rare (e.g. Flux 2008).

Rabbits from other genera, for example *Bunolagus*, *Poelagus* and *Pronolagus,* coexist with hares without physical aggression, and there appear to be no antagonistic interactions between rabbits and jackrabbits (Orr 1940, Flux 2008). However, competition with the black-tailed jackrabbit may affect the distribution of the desert cottontail (AMCELA (Mexican Association for Conservation and Study of Lagomorphs) et al. 2008) and competition may have occurred in at least some areas between the mountain cottontail and the snowshoe hare (Frey & Malaney 2006), although more studies are needed to confirm this interaction. Leporids, for example the black-tailed jackrabbit, eastern cottontail and desert cottontail, may compete with pygmy rabbits for burrows (e.g. Pierce et al. 2011), cape hares may displace the riverine rabbit *Bunolagus monticularis* in marginal habitat (Duthie 1989) and competition between introduced eastern cottontails in Italy and European hares and rabbits is likely, due to marked differences in habitat selection for feeding and resting in sympatric and allopatric areas (Vidus-Rosin et al. 2011, 2012), but has yet to be observed (e.g. Bertolino et al. 2013). In addition, aggressive competitive interactions are documented between the eastern cottontail, brush rabbit and mountain cottontail in North Dakota, USA (Chapman & Verts 1969, Genoways & Jones 1972) and between the eastern cottontail and the forest rabbit in expanding savannah and scrub habitats of South America (Chapman & Flux 1990).

Two species of pika in North America, the American pika *Ochotona princeps* and the collared pika *Ochotona collaris*, show no overlap in range, whereas the ranges of the twenty-three Asian pikas exhibit large degrees of overlap, yet most have no reported interaction in the published literature. The plateau pika *Ochotona curzoniae* excludes the Daurian pika *Ochotona dauurica* and the Gansu pika *Ochotona cansus* from open alpine meadows (Chapman & Flux 1990, Su 2001, Zhang et al. 2001), and Kozlov's pika *Ochotona koslowi* is excluded from the

462 Guldsha valley, Pakistan, by the plateau pika *Ochotona curzoniae* and the Ladak pika *Ochotona*
463 *Ladacensis* (Büchner 1894). In sympatric areas, alpine pikas *Ochotona alpina* and northern pikas
464 *Ochotona hyperborea* compete for shelter, and northern pikas are smaller in sympatry than in
465 allopatry (Chapman & Flux 1990). Interference competition has been reported between Pallas's
466 pikas *Ochotona pallasi* and steppe pikas *Ochotona pusilla* in peak population years (Sokolov et
467 al. 2009). Pallas's pika is more successful due to its aggressiveness and dispersal ability
468 (Smirnov 1974).

469 Two invasive interactions were identified in our literature review: between the European and
470 the mountain hare in Sweden and Ireland (Thulin 2003, Reid, 2011), and between the European
471 hare and the forest rabbit in Argentina (Novillo & Ojeda 2008). Inclusion of these species into
472 the analysis did not have substantial effects on the overall patterns observed; however, we did
473 find that these invasive interactions occupied regions with higher than average human population
474 density and human-converted habitats, and regions which were on average more climatically
475 unstable. Other researchers have found increased occurrence of invasive species in areas of high
476 human population density (e.g. McKinney 2001), and our finding indicates that the interactions
477 between these lagomorph species pairs may be heavily influenced by future human disturbance
478 as well as by climatic changes (e.g. Schmidt et al. 2012). Invasive interactions between the
479 eastern cottontail and native Italian lagomorphs are also possible, however at present there is no
480 available IUCN polygon for the invasive range and competition is yet to be observed (e.g.
481 Bertolino et al. 2013).

482 **Conclusion**

483 Our results have implications for predicting lagomorph responses to global change, and suggest
484 that capturing, parameterizing and incorporating interspecific interactions into analyses may be
485 more important than suggested by the literature, for example, when applying species distribution

modelling (Acevedo et al. 2012). Future behavioural observation studies should focus on areas of sympatry, particularly those areas in which *Lepus* species occur in a narrow contact zone or in species-rich regions (most notably, the hotspots in southern Russia on the border of Mongolia and north western USA), to increase our knowledge of competitive interactions in the order Lagomorpha. The combination of bibliometric analyses and biological data used in this study allowed us to identify traits associated with competitively interacting species and highlight the potential impacts of future environmental change. This approach is widely applicable, and with relatively straightforward methodologies, can provide significant insights into interactions between species.

ACKNOWLEDGEMENTS

This project was funded by Quercus, Northern Ireland's Centre for Biodiversity and Conservation Science supported by the School of Biological Sciences, Queen's University Belfast. We thank Michael Barbour, Kai Collins, Christy Bragg, Deyan Ge, David Hik, Dana Lee, Andrew Smith, Franz Suchentrunk, Zelalem Tolesa and Weihe Yang for contributing species' occurrence data. Particular thanks go to Andrey Lissovsky for taxonomic expertise and for contributing data. We also thank two anonymous reviewers and Nancy Jennings for comments that greatly improved the manuscript.

505 **REFERENCES**

506 Acevedo P, Jimenez-Valverde A, Melo-Ferreira J, Real R, Alves PC (2012) Parapatric species
507 and the implications for climate change studies: a case study on hares in Europe. *Global*
508 *Change Biology* 18: 1509-1519.

509 Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis.
510 *Ecology Letters* 6: 1109-1122.

511 AMCELA (Mexican Association for Conservation and Study of Lagomorphs), Romero Malpica,
512 FJ, Rangel Cordero, H (2008) *Sylvilagus audubonii*. IUCN Red List of Threatened Species.
513 Version 2014.3.

514 Angelici FM, Randi E, Riga F, Trocchi V (2008) *Lepus corsicanus*. IUCN Red List of
515 Threatened Species. Version 2014.3.

516 Anonymous (2003) *GLC 2000: Global Land Cover Mapping for the Year 2000*. European
517 Commission Joint Research Centre, Institute for Environment and Sustainability.
518 Available at: http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php.

519 Bakker ES, Olff H, Gleichman JM (2009) Contrasting effects of large herbivore grazing on
520 smaller herbivores. *Basic and Applied Ecology* 10: 141-150.

521 Bertolino S, Cordero di Montezemolo N, Perrone A (2013) Habitat use of coexisting introduced
522 eastern cottontail and native European hare. *Zeitschrist für Säugetierkunde* 78: 235-240.

523 Best TL, Henry TH (1993) *Lepus callotis*. *American Society of Mammologists, Mammalian*
524 *Species* 442: 1-6.

525 Birch LC (1957) The meanings of competition. *American Naturalist* 91: 5-18.

526 Brooke ZM, Bielby J, Nambiar K, Carbone C (2014) Correlates of research effort in carnivores:
527 body size, range size and diet matter. *PLOS ONE*, 9: e93195.

528 Brown JH, Maurer BA (1986) Body size, ecological dominance and Cope's rule. *Nature* 324:
529 248-250.

530 Büchner E (1894) Wissenschaftliche Resultate der von N. M. Przewalski nach central-Asien
531 unternommenen Reisen auf Kosten einer von seiner Kaiserliche Hoheit dem Grossfursten
532 Thronfolger Nikolai Alexandrowitsh gespendeten Summe herausgegeben von der
533 Kaiserlichen Akademie der Wissenschaften St. Petersburg. Zoologischer, Theil. Band I.
534 *Saugethiere* 5: 185-232.

535 Bull CM (1991) Ecology of parapatric distributions. *Annual Review of Ecology and Systematics*
536 22: 19-36.

537 Caravaggi A, Montgomery WI, Reid N (2014) Range expansion and comparative habitat use of
538 insular, congeneric lagomorphs: invasive European hares *Lepus europaeus* and endemic Irish
539 hares *Lepus timidus hibernicus*. *Biological Invasions*, 17: 687-698.

540 Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community
541 ecology and phylogenetic biology. *Ecology Letters* 12: 693-715.

542 Chaneton EJ, Bonsall MB (2000) Enemy-mediated apparent competition: empirical patterns and
543 the evidence. *Oikos* 88: 380-394.

544 Chapman JA, Flux JEC (1990) *Rabbits, Hares and Pikas: Status Survey and Conservation*
545 *Action Plan*. IUCN, Gland, Switzerland.

546 Chapman JA, Flux JEC (2008) Introduction to the Lagomorpha. In: Alves PC, Ferrand N,
547 Hackländer K (eds) *Lagomorph Biology: Evolution, Ecology and Conservation,* 1-9.
548 Springer-Verlag Berlin Heidelberg, Germany.

549 Chapman JA, Verts BJ (1969) Interspecific aggressive behaviours in rabbits. *Murrelet* 50: 17-18.

550 Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case
551 TJ (2002) The interaction between predation and competition: a review and synthesis.
552 *Ecology Letters* 5: 302-315.

553 Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species
554 associated with high levels of climate warming. *Science* 333: 1024-1026.

555 Cheng E, Hodges KE, Melo-Ferreira J, Alves PC, Mills LS (2014) Conservation implications of
556 the evolutionary history and genetic diversity hotspots of the snowshoe hare. *Molecular*
557 *Ecology* 23: 2929-2942.

558 Connell JH (1983) On the prevalence and relative importance of interspecific competition:
559 evidence from field experiments. *American Naturalist* 122: 661-696.

560 Cornell HV, Lawton JH (1992) Species interactions, local and regional processes and limits to
561 the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*
562 61: 1-12.

563 Cox R (1976) A day in the life of a rabbiter. *NZ Outdoor* 41: 23-25.

564 Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of*
565 *Favoured Races in the Struggle for Life*. Murray, London, UK.

566 Day JJ, Cotton JA, Barraclough TG (2008) Tempo and mode of diversification of Lake
567 Tanganyika Cichlid Fishes. *PLOS ONE* 3: e1730.

568 DeCesare NJ, Hebblewhite N, Robinson HS, Musiani M (2010) Endangered, apparently: the role
569 of apparent competition in endangered species conservation. *Animal Conservation* 13: 353-
570 362.

571 Duthie AG (1989) The ecology of the riverine rabbit (*Bunolagus monticularis*). MSc thesis,
572 University of Pretoria, South Africa.

573 Fa JE, Bell DJ (1990) Chapter 12: The volcano rabbit *Romerolagus diazi*. In: Chapman JA, Flux
574 JC (eds) *Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan*, 143-146.
575 IUCN, Gland, Switzerland.

576 Fadeev VA (1966) The diet and daily rhythms of the brown hare in western Kazahkstan. *Nauka*,
577 Moscow-Leningrad, Russian Federation.

578 Flinders JT, Chapman JA (2003) Chapter 6: Black-tailed Jackrabbit. In: Feldhammer GA,
579 Thompson BC, Chapman JA (eds) *Wild Mammals of North America: Biology, Management*
580 *and Conservation*, 126-146. John Hopkins University Press, Baltimore, Maryland, USA.

581 Flux JEC (1981) Field observations of behaviour in the genus *Lepus*. In: Myers K, MacInnes CD
582 (eds) *Proceedings of the World Lagomorph Conference*, University of Guelph, Guelph,
583 Canada, 337-394.

584 Flux JEC (1994) World distribution. In: Thompson HV, King CM (eds) *The European Rabbit.*
585 *The History and Biology of a Successful Coloniser*, 8-17. Oxford University Press, Oxford,
586 UK.

587 Flux JEC (2008) A review of competition between rabbits (*Oryctolagus cuniculus*) and hares
588 (*Lepus europaeus*). In: Alves PC, Ferrand N, Hackländer K (eds) *Lagomorph Biology:*
589 *Evolution, Ecology and Conservation,* 241-249. Springer-Verlag Berlin Heidelberg,
590 Germany.

591 Frey JK, Malaney JL (2006) Snowshoe hare (*Lepus americanus*) and mountain cottontail
592 (*Sylvilagus nuttallii*) biogeography at their southern range limit. *Journal of Mammalogy* 87:
593 1175-1182.

594 Fritz SA, Bininda-Emonds OR, Purvis A (2009) Geographical variation in predictors of
595 mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* 12: 538-549.

596 Gayot E (1868) Lievres, alpins et leporids. *Comptes rendus de l'Academie des sciences* 12: 1-
597 456.

598 Ge D, Wen Z, Xia L, Zhang Z, Erbajeva M, Huang C, Yang Q (2013) Evolutionary history of
599 lagomorphs in response to global environmental change. *PLOS ONE* 8: e59668.

600 Genoways HH, Jones Jr JK (1972) Mammals from south-western North Dakota. *Occasional*
601 *Papers, Museum of Texas Tech University* 6: 1-36.

602 Gortázar C, Millán J, Acevedo P, Escudero MA, Marco J, Fernández de Luco D (2007) A large-
603 scale survey of brown hare *Lepus europaeus* and Iberian hare *L. granatensis* populations at
604 the limit of their ranges. *Wildlife Biology* 13: 244-250.

605 Gutiérrez EE, Boria RA, Anderson RP (2014) Can biotic interactions cause allopatry? Niche
606 models, competition and distributions of South American mouse opossums. *Ecography* 37:
607 741-753.

608 Hackländer K, Ferrand N, Alves PC (2008) Overview of lagomorph research: what we have
609 learned and what we still need to do. In: Alves PC, Ferrand N, Hackländer K (eds)
610 *Lagomorph Biology: Evolution, Ecology and Conservation,* 381-391. Springer-Verlag Berlin
611 Heidelberg.

612 Hatcher MJ, Dick JTA, Dunn AM (2006) How parasites affect interactions between competitors
613 and predators. *Ecology Letters* 9: 1253-1271.

614 Hewson R (1990) Interactions between mountain hares (*Lepus timidus*) and other mammals.
615 *Journal of Zoology* 221: 302-305.

616 Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global
617 disparities of habitat loss and protection. *Ecology Letters* 8: 23–29.

618 Huey RB (1979) Parapatry and niche complementarity of Peruvian Desert Geckos
619 (*Phyllodactylus*): the ambiguous role of competition. *Oecologia* 38: 249-259.

620 Hulbert IAR, Andersen R (2001) Food competition between a large ruminant and a small
621 hindgut fermentor: the case of the roe deer and mountain hare. *Oecologia* 128: 499-508.

622 Iwamura T, Guisan A, Wilson KA, Possingham HP (2013) How robust are global conservation
623 priorities to climate change? *Global Environmental Change* 23: 1277-1284.

624 Jankowski JE, Robinson SK, Levey DJ (2010) Squeezed at the top: interspecific aggression may
625 constrain elevational ranges in tropical birds. *Ecology* 91: 1877-1884.

626 Johnston JE (1972) Identification and distribution of cottontail rabbits in southern New England.
627 MS Thesis, University of Connecticut, Storrs.

628 Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL et al. (2009) PanTHERIA: a
629 species-level database of life history, ecology and geography of extant and recently extinct
630 mammals. *Ecology* 90: 2648.

631 Katona K, Biro Z, Hahn I, Kertész M, Altbäcker V (2004) Competition between European hare
632 and European rabbit in a lowland area, Hungary: a long-term ecological study in the period
633 of rabbit extinction. *Folia Zoology* 53: 255-268.

634 Keddy PA (2001) *Competition* (2nd edition). Kluwer Academic Publishers, Dordrecht.

635 Koblmüller S, Wayne RK, Leonard JA (2012) Impact of Quartenary climatic changes and
636 interspecific competition on the demographic history of a highly mobile generalist carnivore,
637 the coyote. *Biology Letters* 8: 644-647.

638 Leopold A (1947) The distribution of Wisconsin hares. *Transactions of the Wisconsin Academy*
639 *of Sciences, Arts and Letters* 37: 1-14.

640 Leyequien E, de Boer WF, Cleef A (2007) Influence of body size on coexistence of bird species.
641 *Ecological Research* 22: 735-741.

642 Lind EA (1963) Observations on the mutual relationship between the snow hare (*Lepus timidus*)
643 and the field hare (*L.europaeus*). *Suomen Riista* 16: 128-135.

644 Litvaitis JA, Barbour MS, Brown AL, Kovach AI, Litvaitis MK, Oehler JD, Probert BL, Smith
645 DF, Tash JP, Villafuerte R (2008) Testing multiple hypotheses to identify causes of the
646 decline of a lagomorph species: the New England cottontail as a case study. In: Alves PC,
647 Ferrand N, Hackländer K (eds) *Lagomorph Biology: Evolution, Ecology and Conservation,*
648 167-185. Springer-Verlag Berlin Heidelberg, Germany.

649 Liu J, Yu L, Arnold ML, Wu C-H, Wu S-F, Lu X, Zhang Y-P (2011). Reticulate evolution:
650 frequent introgressive hybridization among Chinese hares (genus *Lepus*) revealed by
651 analyses of multiple mitochondrial and nuclear DNA loci. *BMC Evolutionary Biology* 11:
652 223-237.

653 Luiselli L (2006) Resource partitioning and interspecific competition in snakes: the search for
654 general geographical and guild patterns. *Oikos* 114: 193-211.

655 McCain CM, King SRB (2014) Body size and activity times mediate mammalian responses to
656 climate change. *Global Change Biology* 20: 1760-1769.

McCann K (2007) Protecting biostructure. *Nature* 446: 29.

McCarthy MP, Best MJ, Betts RA (2010) Climate change in cities due to global warming and urban effects. *Geophysical Research Letters* 37: L09705.

McKinney ML (2001) Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation* 100: 243-252.

Melo-Ferreira J, Alves PC, Freitas H, Ferrand N, Boursot P (2009) The genomic legacy from the extinct *Lepus timidus* to the three hare species of Iberia: contrast between mtDNA, sex chromosomes and autosomes. *Molecular Ecology* 18: 2643-2658.

Melo-Ferreira J, Seixas FA, Cheng E, Mills LS, Alves PC (2014) The hidden history of the snowshoe hare, *Lepus americanus*: extensive mitochondrial DNA introgression inferred from multilocus genetic variation. *Molecular Ecology* 23: 4617-4630.

Millais JG (1906) The mammals of Great Britain and Ireland. Longmans, Green & Co, London.

Mills LS, Zimova M, Oyler J, Running S, Abatzoglou JT, Lukacs PM (2013) Camouflage mismatch in seasonal coat colour due to decreased snow duration. *PNAS* 110: 7360-7365.

Ness JH, Bressmer K (2005) Abiotic influences on the behaviour of rodents, ants, and plants affect an ant-seed mutualism. *Ecoscience* 12: 76-81.

Novillo A, Ojeda RA (2008) The exotic mammals of Argentina. *Biological Invasions* 10: 1333-1344.

Orr RT (1940) The rabbits of California. *Occasional Papers of the California Academy of Sciences* 19: 1-227.

Paradis E, Blomberg S, Bolker B, Claude J, Cuong HS, Desper R et al. (2014) ape: Analyses of phylogenetics and evolution. R Package version 3.0-11.

679 Petrovan SO (2011) The landscape ecology of brown hares and European rabbits in pastures in
680 the north east of England. PhD thesis, University of Hull, Hull, UK.

681 Pierce JE, Larsen RT, Flinders JT, Whiting JC (2011) Fragmentation of sagebrush communities:
682 does an increase in habitat edge impact pygmy rabbits? *Animal Conservation* 14: 314-321.

683 Pietri C, Alves PC, Melo-Ferreira J (2011) Hares in Corsica: high prevalence of Lepus
684 corsicanus and hybridization with introduced *L.europaeus* and *L.granatensis*. *European*
685 *Journal of Wildlife Research* 57: 313-321.

686 Post E (2013) *Ecology of Climate Change: the importance of biotic interactions*. Princeton
687 University Press, Princeton, New Jersey, USA.

688 Probert BL, Litvaitis JA (1996) Behavioural interactions between invading and endemic
689 lagomorphs: implications for conserving a declining species. *Biological Conservation* 76:
690 289-296.

691 Reid N, Montgomery WI (2007) Is naturalisation of the brown hare in Ireland a threat to the
692 endemic Irish hare? *Biology and Environment: Proceedings of the Royal Irish Academy*
693 107b: 129-138.

694 Reid N (2011) European hare (*Lepus europaeus*) invasion ecology: implication for the
695 conservation of the endemic Irish hare (*Lepus timidus hibernicus*). *Biological Invasions* 13:
696 559-569.

697 Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. *Annual Review*
698 *in Ecology and Systematics* 27: 83-109.

699 Schmidt JA, McCleery R, Seavey JR, Cameron Devitt SE, Schmidt PM (2012) Impacts of a half
700 century of sea-level rise and development on an endangered mammal. *Global Change*
701 *Biology* 18: 3536-3542.

702 Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging
703 processes in mechanistic urban ecology. *Trends in Ecology and Evolution* 21: 186-191.

704 Schoener TW (1982) The controversy over interspecific competition. *American Scientist* 70:
705 586-595.

706 Schoener TW (1983) Field experiments on interspecific competition. *American Naturalist* 122:
707 240-285.

708 Smirnov PK (1974) Biotopic distribution and territorial relationship of the steppe and Pallas'
709 pika in the sympatric zone of their ranges. *Byulleten' Moskovskogo Obshchestva Ispytatelei*
710 *Prirody Otdel Biologicheskii* 75: 72-80.

711 Smith AT, Xie Y (2008) *A Guide to the Mammals of China*. Princeton University Press,
712 Princeton, New Jersey, USA.

713 Smith DF, Litvaitis JA (1999) Differences in eye size and predator-detection distances of New
714 England and eastern cottontails. *Northeast Wildlife* 54: 55-60.

715 Smith DF, Litvaitis JA (2000) Foraging strategies of sympatric lagomorphs: implications for
716 differential success in fragmented landscapes. *Canadian Journal of Zoology* 78: 2134-2141.

717 Sokolov VE, Ivanitskaya EY, Gruzdev VV, Heptner VG, Hoffmann RS, Smith AT (2009)
718 *Lagomorphs: mammals of Russia and adjacent regions*. CRC Press, Boca Raton, Florida,
719 USA.

720 Somers N, Milotic T, Hoffmann M (2012) The impact of sward height, forage quality and
721 competitive conditions on foraging behaviour of free-ranging rabbits (*Oryctolagus cuniculus*
722 L.). *Belgian Journal of Zoology* 142: 74-85.

723 Su JP (2001) A comparative study on the habitat selection of plateau pika (*Ochotona curzoniae*)
724 and Gansu pika (*Ochotona cansus*). PhD thesis, Northwest Plateau Institute of Biology,
725 Xining, Qinghai, China.

726 Tafani M, Cohas A, Bonenfant C, Gaillard J-M, Allainé D (2013) Decreasing litter size of
727 marmots over time: a life history response to climate change? *Ecology* 94: 580-586.

728 Thulin C-G (2003) The distribution of mountain hares *Lepus timidus* in Europe: a challenge
729 from brown hares *L.europaeus*? *Mammal Review* 33: 29-42.

730 Thulin C-G, Tegelström H (2002) Biased geographical distribution of mitochondrial DNA that
731 passed the species barrier from mountain hares to brown hares (genus *Lepus*): an effect of
732 genetic incompatibility and mating behaviour? *Journal of Zoology* 258: 299-306.

733 Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species
734 interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351-1363.

735 Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AO (2011) Chapter 14: Measuring
736 phylogenetic diversity. In: Magurran AE, McGill BJ (eds) 193-206. *Biological Diversity:*
737 *Frontiers in Measurement and Assessment.* Oxford University Press, Oxford, UK.

738 Venail PA, Narwani A, Fritschie K, Alexandrou MA, Oakley TH, Cardinale BJ (2014) The
739 influence of phylogenetic relatedness on species interactions among freshwater green algae
740 in a mesocosm experiment. *Journal of Ecology* 102: 1288-1299.

741 Vidus-Rosin A, Gilio N, Meriggi A (2008) Introduced lagomorphs as a threat to 'native'
742 lagomorphs: the case of the Eastern cottontail (*Sylvilagus floridanus*) in Northern Italy. In:
743 Alves PC, Ferrand N, Hackländer K (eds) *Lagomorph Biology: Evolution, Ecology and*
744 *Conservation,* 153-165. Springer-Verlag Berlin Heidelberg.

745 Vidus-Rosin A, Meriggi A, Cardarelli E, Serrano-Perez S, Mariani M-C, Corradelli C, Barba A
746 (2011) Habitat overlap between sympatric European hares (*Lepus europaeus*) and Eastern
747 cottontails (*Sylvilagus floridanus*) in northern Italy. *Acta Theriologica* 56: 53-61.

748 Vidus-Rosin A, Lizier L, Meriggi A, Serrano-Perez S (2012) Habitat selection and segregation
749 by two sympatric lagomorphs: the case of European hares (*Lepus europaeus*) and
750 Eastern cottontails (*Sylvilagus floridanus*) in northern Italy. *Acta Theriologica* 57: 295-
751 304.

752 Violle C, Nemergut DR, Pu Z, Jiang L (2011) Phylogenetic limiting similarity and competitive
753 exclusion. *Ecology Letters* 14: 782-787.

754 Watson JEM, Iwamura T, Butt N (2013) Mapping vulnerability and conservation adaptation
755 strategies under climate change. *Nature Climate Change* 3: 989-994.

756 Wilson CC, Bernatchez L (1998) The ghost of hybrids past: fixation of arctic charr (*Salvelinus*
757 *alpinus*) mitochondrial DNA in an introgressed population of lake trout (*S. namaycush*).
758 *Molecular Ecology* 7: 127-132.

759 Zhang D, Fan N, Yin H (2001) Comparative analysis of behaviour between *Ochotona dauurica*
760 and *Ochotona curzoniae* in sympatric coexistence. *Journal of Hebei University, Natural*
761 *Science Edition* 21: 72-77.

762

763 **Table 1.** Summary of the 33 competitive interactions documented in the order Lagomorpha,
764 involving 33 species. Type of competitive interaction (exploitation or interference), resource
765 competing for, and a citation for the interaction are also listed. Invasive interactions are
766 highlighted in bold.

767

Competition	For…	Species	Replaced by…	Citation
Exploitation	Habitat	*Brachylagus idahoensis*	*Lepus californicus*	Pierce et al. 2011
Exploitation	Habitat	*Brachylagus idahoensis*	*Sylvilagus audubonii*	Pierce et al. 2011
Exploitation	Habitat	*Bunolagus monticularis*	*Lepus capensis*	Duthie 1989
Exploitation	Habitat	*Lepus alleni*	*Lepus californicus*	Chapman & Flux 1990
Exploitation	Habitat	*Lepus americanus*	*Lepus townsendii*	Leopold 1947
Exploitation	Habitat	*Lepus americanus*	*Sylvilagus nuttallii*	Frey & Malaney 2006
Exploitation	Habitat	*Lepus callotis*	*Lepus californicus*	Best & Henry 1993
Exploitation	Habitat	*Lepus capensis*	*Lepus habessinicus*	Flux 2008
Exploitation	Habitat	*Lepus capensis*	*Lepus europaeus*	Chapman & Flux 1990
Exploitation	Habitat	*Lepus corsicanus*	*Lepus europaeus*	Angelici et al. 2008
Exploitation	Habitat	*Lepus europaeus*	*Lepus tolai*	Sokolov et al. 2009
Exploitation	Habitat	*Lepus europaeus*	*Lepus granatensis*	Gortázar et al. 2007
Exploitation	Habitat	*Lepus habessinicus*	*Lepus microtis*	Chapman & Flux 1990
Exploitation	Habitat	*Lepus habessinicus*	*Lepus saxatilis*	Chapman & Flux 1990
Exploitation	Habitat	*Lepus habessinicus*	*Lepus fagani*	Chapman & Flux 1990
Exploitation	Habitat	*Lepus mandshuricus*	*Lepus tolai*	Chapman & Flux 1990, Smith & Xie 2008
Exploitation	Habitat	*Lepus microtis*	*Lepus saxatilis*	Flux 2008
Exploitation	Habitat	***Lepus timidus***	***Lepus europaeus***	**Thulin 2003, Reid 2011**
Exploitation	Habitat	*Lepus townsendii*	*Lepus californicus*	Flinders & Chapman 2003
Exploitation	Habitat	*Ochotona cansus*	*Ochotona curzoniae*	Chapman & Flux 1990
Exploitation	Habitat	*Ochotona dauurica*	*Ochotona curzoniae*	Zhang et al. 2001
Exploitation	Habitat	*Ochotona koslowi*	*Ochotona curzoniae*	Buchner 1894
Exploitation	Habitat	*Ochotona koslowi*	*Ochotona ladacensis*	Buchner 1894
Exploitation	Habitat	*Sylvilagus audubonii*	*Lepus californicus*	AMCELA (Mexican Association for Conservation and Study of Lagomorphs) et al. 2008
Exploitation	Habitat	*Sylvilagus audubonii*	*Lepus callotis*	Best & Henry 1993
Exploitation	Habitat	***Sylvilagus brasiliensis***	***Lepus europaeus***	**Novillo & Ojeda 2008**
Exploitation	Shelter	*Ochotona hyperborea*	*Ochotona alpina*	Chapman & Flux 1990
Interference	Habitat	*Brachylagus idahoensis*	*Sylvilagus floridanus*	Pierce et al. 2011
Interference	Habitat	*Ochotona pusilla*	*Ochotona pallasi*	Sokolov et al. 2009
Interference	Habitat	*Sylvilagus bachmani*	*Sylvilagus floridanus*	Chapman & Verts 1969
Interference	Habitat	*Sylvilagus brasiliensis*	*Sylvilagus floridanus*	Chapman & Flux 1990
Interference	Habitat	*Sylvilagus nuttallii*	*Sylvilagus floridanus*	Genoways & Jones 1972
Interference	Habitat/food	*Sylvilagus transitionalis*	*Sylvilagus floridanus*	Probert & Litvaitis 1996, Litvaitis et al. 2008

768

Figures

Fig. 1.

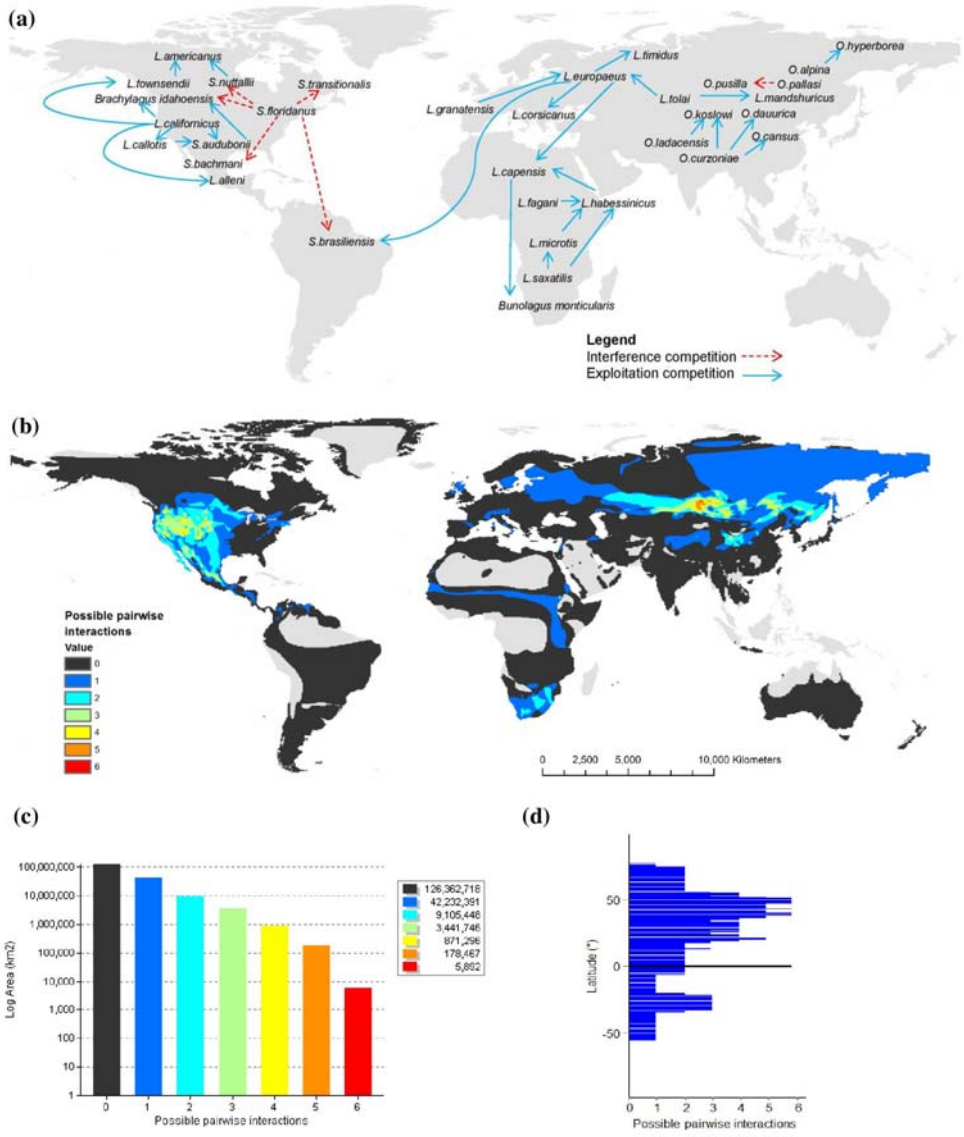
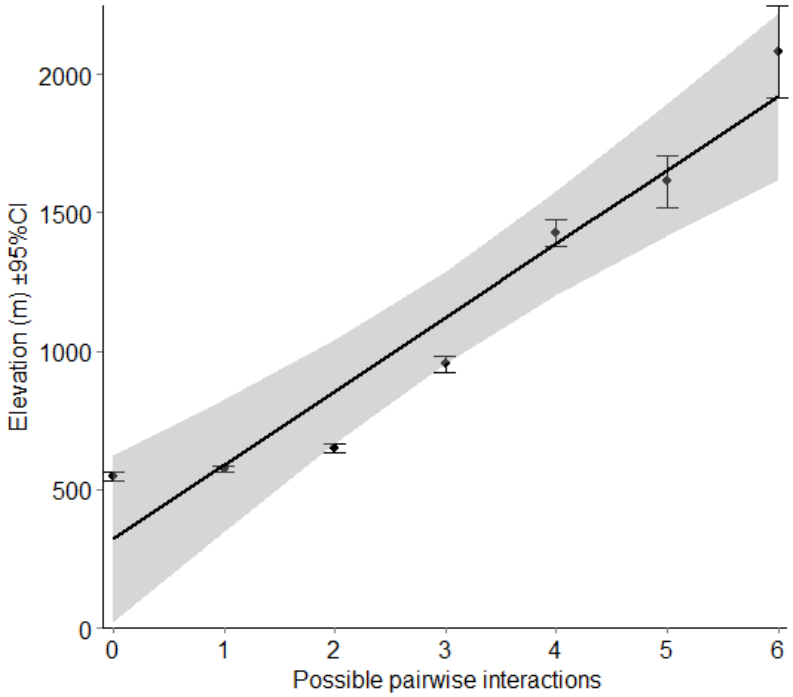


Figure 1. (a) Documented competitive interactions in the order Lagomorpha shown in their approximate geographic locations. Red arrows (dashed) indicate interference competition, blue arrows indicate exploitation competition. **(b)** Global distribution of possible pairwise competitive interactions between the 33 species in the order Lagomorpha that have documented interactions with other species. Pale grey areas indicate places where no lagomorph species are found. **(c)** Histogram of the area occupied by possible pairwise interactions between species documented to interact with others. **(d)** Histogram of the latitudes occupied by possible pairwise

778 interactions between species known to interact with others; the bold line represents the Equator.
779 In (b), (c) and (d), zero possible pairwise interactions indicates the occurrence of one species not
780 documented to interact with others.

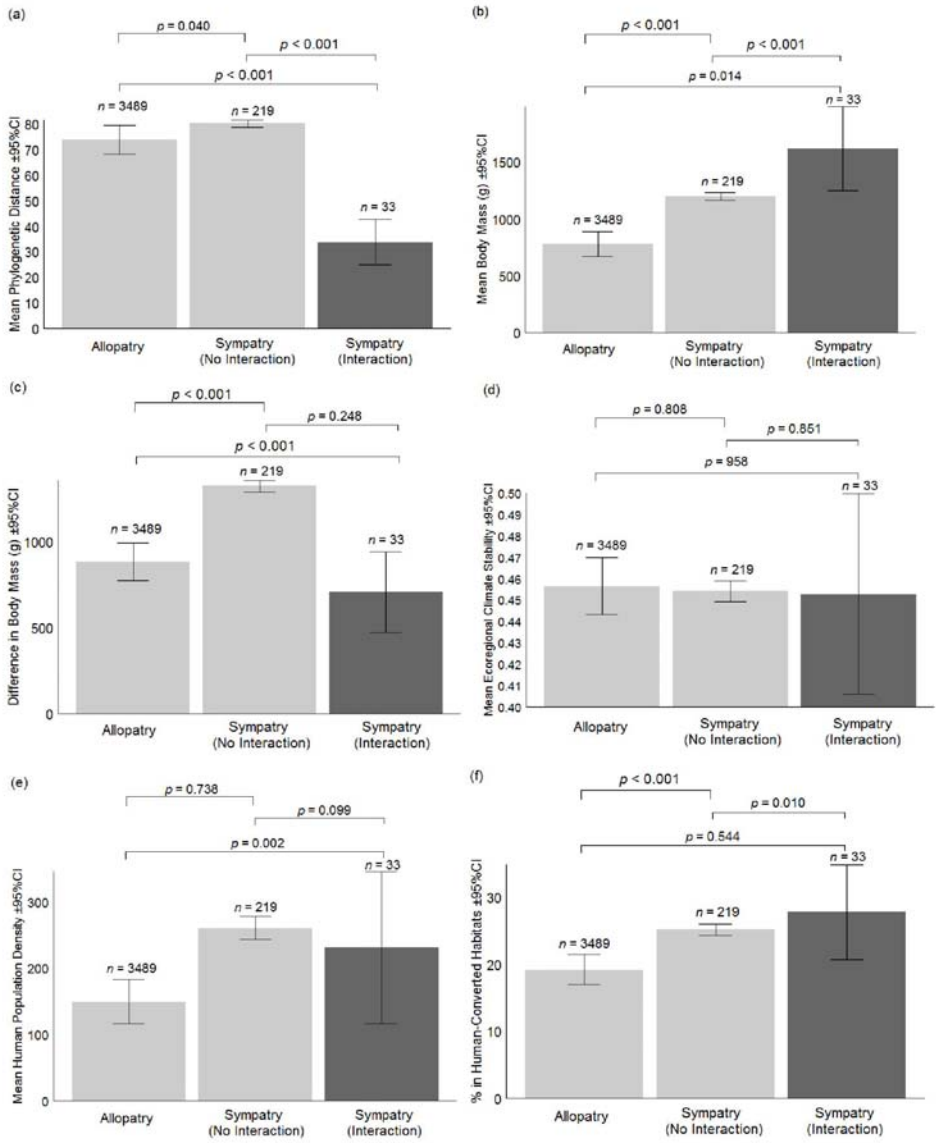
781



782

783 **Figure 2.** Relationship between possible pairwise interactions in species of Lagomorpha
784 documented to interact with others and elevation (m), with ± 95% confidence error bars. The
785 grey area surrounding the fitted linear regression line indicates the 95% confidence limits.

Fig. 3.



786

787 **Figure 3.** Mean phylogenetic distance **(a)**, mean body mass **(b)**, difference in body mass
788 between each species in an interacting pair **(c)**, mean ecoregional climate stability **(d)**, mean
789 human population density **(e)** and mean percentage of occurrence records in human-converted
790 habitats **(f)** ±95% confidence intervals, for lagomorph species in allopatry (light grey), sympatry
791 with no known interaction (light grey) and sympatry with an interaction (dark grey).

792

SUPPORTING INFORMATION

Appendix S1. Variables considered, but not included in the analysis.

- Activity cycle,
- Body length,
- Body mass at birth,
- Diet breadth,
- Elevational change (1930-2080),
- Gestation length,
- Habitat breadth,
- Home range size,
- Land use change (1980-2050),
- Land use change (1980-2070),
- Litter size,
- Litters per year,
- Poleward movement (1930-2080),
- Population density,
- Range decline (1930-2080).

Appendix S2. Results of Generalized Linear Models characterising phylogenetic distance, body mass, difference in body mass, ecoregional climatic stability, human population density and percentage of occurrence records in human-converted habitats for pairs of species of lagomorph in allopatry, sympatry with no interaction and sympatry with an interaction. Significant *p* values are in bold.

Response variable	Term	β ± s.e.	*t*	*p*
Mean phylogenetic distance $F_{2, 3738}$=19.80 (p<0.001)	Sympatry-Interaction & Sympatry-No Interaction	39.971 ± 7.791	5.130	**<0.001**
	Sympatry-Interaction & Allopatry	-46.311 ± 7.729	-5.992	**<0.001**
	Sympatry-No Interaction & Allopatry	-6.340 ± 3.078	-2.060	**0.040**
Mean adult body mass (g) $F_{2, 3738}$=22.26 (p<0.001)	Sympatry-Interaction & Sympatry-No Interaction	-838.100 ± 162.500	-5.159	<**0.001**
	Sympatry-Interaction & Allopatry	419.790 ± 170.930	2.456	**0.014**
	Sympatry-No Interaction & Allopatry	-418.300 ± 68.080	-6.144	**<0.001**
Difference in adult body mass (g) $F_{2, 3738}$=26.81 (p<0.001)	Sympatry-Interaction & Sympatry-No Interaction	176.100 ± 152.000	1.159	0.248
	Sympatry-Interaction & Allopatry	-616.590 ± 171.230	-3.601	**<0.001**
	Sympatry-No Interaction & Allopatry	-440.470 ± 68.200	-6.458	**<0.001**
Mean ecoregional climate stability $F_{2, 3738}$=0.03 (p=0.969)	Sympatry-Interaction & Sympatry-No Interaction	0.004 ± 0.020	0.188	0.851
	Sympatry-Interaction & Allopatry	-0.001 ± 0.025	-0.053	0.958
	Sympatry-No Interaction & Allopatry	0.002 ± 0.010	0.243	0.808
Mean human population density $F_{2, 3738}$=5.02 (p<0.001)	Sympatry-Interaction & Sympatry-No Interaction	-81.760 ± 49.480	-1.653	0.099
	Sympatry-Interaction & Allopatry	-29.580 ± 88.508	-0.334	0.738
	Sympatry-No Interaction & Allopatry	-111.342 ± 35.253	-3.158	**0.002**
Mean % of occurrence records in human-converted habitats $F_{2, 3738}$=6.30 (p=0.002)	Sympatry-Interaction & Sympatry-No Interaction	-8.538 ± 3.269	-2.612	**0.010**
	Sympatry-Interaction & Allopatry	2.600 ± 4.283	0.607	0.544
	Sympatry-No Interaction & Allopatry	-5.940 ± 1.706	-3.482	**<0.001**